

DYNAMIC EQUILIBRIA IN THE SOIL

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So many studies in soil microbiology have been concerned with counting or with listing the organisms present in the soil that an impression has arisen that the soil is essentially a static system. The very stability of the soil population re-enforces this idea. It is important therefore to emphasize from time to time that this stability is the stability of a dynamic equilibrium. An equilibrium in which the individual units of the system are constantly changing, but compensating changes in other components maintain the over-all balance. The most familiar example of this is the nitrogen cycle where interconversions between free nitrogen, nitrates, nitrites, proteins, ammonia, etc., take place, where nitrogen is lost by leaching or added by biological or electrical fixation, yet despite all these changes the over-all amount of nitrogen in a natural system remains relatively constant, as indeed do the amounts of the individual components. Because of the great stress which has been laid on the nitrogen cycle both in teaching and in agriculture, the importance of other interchanges is often overlooked.

In soil mycology the changes associated with the annual leaf and branch fall are an outstanding example of a dynamic equilibrium so far as the soil is concerned. Several studies have given quantitative data on the changes involved, and they all give a similar picture provided the system being studied has reached the stable condition. Blow (1955) examined in detail the litter and litter fall in oakwoods in America. He showed that just before leaf and branch fall began, the amount of litter on the soil surface corresponded to about 4·2 tons per acre. Fall of leaves started in August, and the amount of new litter reached a maximum in December and January. The freshly fallen litter amounted to 1·4 tons per acre. Rapid decomposition occurred during the winter and early spring, so that although the amount of litter had risen to over 5 tons per acre immediately following leaf fall, by July it was back again to the summer value of 4·2 tons per acre. Observations on pine litter in England and the litter from stands of *Casuarina* in Australia show similar changes. The decomposition and leaching losses balance the

annual increment from leaf fall; litter addition and decomposition are in a state of dynamic equilibrium.

In Blow's work the annual fall was 1·4 tons per acre, whereas in some tropical forests it may reach 30 tons per acre, but even under these conditions decomposition is sufficiently rapid to prevent any marked accumulation.

The above work refers to the over-all picture. If a single leaf is considered, a wide range of variation is seen. A leaf falling in a tropical rain-forest may be completely disintegrated in less than three months, but a pine needle in a Northern European forest takes 6–7 years at least before it is completely disintegrated. Despite this long period of decay, in a well-established pine forest the amount of litter does not change appreciably from year to year. Again, an amount of litter equal to the annual leaf fall is decomposed or leached away each year. Failure to appreciate this has led to many confusions, and particularly in connexion with discussions on mull and mor. It is frequently stated that decomposition is rapid in mull and slow in mor humus. While it is true that an individual oak leaf falling on to a mull soil may be decomposed in a year and a pine needle on mor may take 7–8 years to reach a similar state, in mature stands both systems may decompose comparable amounts of material per year. It is similar to an observer watching two trains pass, both travelling at the same speed but one with a single carriage, the other with thirty. The observer still sees the long train for some time after the short one has passed, although both were travelling at the same speed. Decomposition in mull and mor has many features in common with the two trains.

In studying the dynamic equilibria in the soil, we need to know the rates of the individual changes in the system and the nature of the compensating processes. The annual burst of decomposition associated with leaf fall is accompanied by an increase in microbiological activity, and it might be expected that this activity would be reflected in the changes in the number of micro-organisms present. Protozoal and bacterial numbers do fluctuate rapidly, and in some studies at least there is evidence of big increases in the populations of these organisms associated with the availability of fresh food reserves. Only occasionally has evidence for comparable fluctuations in fungal numbers been obtained. This may be because of the relatively long life of the fungal hypha or spore, compared with a bacterial or protozoal cell.

Our knowledge of the functional life of an individual fungal hypha is very meagre. In Rossi-Cholodny slides one can often see phycomycetous hyphae with densely cytoplasmic tips. A short distance back from the

tips the cytoplasm becomes vacuolate, and farther back still the hyphae appear empty and are often enveloped in bacteria which seem to lyse the cell walls, leaving only slight traces of the hyphae. The evidence suggests that this kind of fungus progressively explores the soil, gradually accumulating a mass of cytoplasm at the growing tips until fruiting can be achieved. In an agricultural soil with a high bacterial count, the life of any individual piece of hypha is of the order of one or two days. This evidence is based on Rossi-Cholodny slides which represent somewhat artificial conditions; nevertheless, the available field evidence suggests that the time scale is of the right order. Warcup (1957), in his studies of Australian wheat-fields, found that *Rhizopus* and *Mortierella* produced sporangia 3 days after rain had fallen following the normal summer dry spell. The evidence here strongly suggests that from spore germination to sporing was 3 days. The fate of the vegetative hyphae was not recorded. Experience with Phycomycetes generally suggests that once sporing has been accomplished the vegetative hyphae cease to function, and in natural substrates such as dung or in composts, the hyphae are rapidly disintegrated. It is natural to think of each spore germinating, producing a mycelium with numerous sporangia each containing many spores, leading to a many hundred-fold increase. If this happens, then such increases ought to lead to tremendous and sudden variations in the number of colonies recorded in dilution-plate studies of such soils. The increases recorded, however, are surprisingly small, and an increase of the plate count by a factor of 20 represents one of the largest recorded. There may be several reasons why the increase is relatively slight. The general fungistasis may be very effective, and although one spore might give rise to 20,000 or so after a few days, if the initial population were of the order of 4,000 the germination and reproduction of only 9 spores out of the 4,000 would give a tenfold increase in the population.

Alternatively, it may be that when fresh substrates become available, a large proportion of spores lying dormant in the soil germinate and produce a mycelium which gives a greatly increased number of new spores, but these are quickly eliminated either by lysis, ingestion, or some other rapidly acting agency. At present we know practically nothing about the rate of destruction of spores. A third possibility is that the amounts of food materials immediately available at any one time are so small that any particular mycelium may produce only a few depauperate sporangia. Certainly when sporangia of mucors or sporing heads of Penicillia have been observed in the soil, they are very reduced when compared with the fruiting structures met in culture.

The life of Ascomycete and Basidiomycete mycelium seems to be very

different. Growth rates, on the whole, are slower and hyphae function for greater periods. It is interesting that Phycomycetes as a group do not produce antibiotics and disintegration of their hyphae is often recorded. The long-lived mycelium of the Basidiomycetes, many of which produce antibiotics, seldom appears to be attacked by bacteria. Disintegration of the mycelium of Ascomycetes, Fungi Imperfecti, and Basidiomycetes seems to be accomplished more often by small animals such as mites and collembolas than by bacteria.

The above situations might be termed 'normal', where the hyphae when they have ceased to function are broken down. Abnormal situations also occur. Romell long ago showed that in mor humus there were characteristically large masses of relict mycelium. An extreme case is that investigated by Hepple (1958), who showed that in the B₁ of a podzol investigated by her a great deal of the hyphae had become virtually mummified by encrusting humic acid.

It is often very difficult to decide how many of the hyphae present in the soil are still active. Warcup (1957) found that on an average about 23% of the hyphae dissected from the soil were viable. This value rose to 75% soon after the crop residues were ploughed in, and fell to 3–15% during the dry summer. When the soil dries out below the wilting point most hyphae are killed, but clearly some can survive, as shown by Warcup, even for 6–8 weeks at a relative humidity of 30–50%. Such low humidity will also kill many spores. In Warcup's data we can see that a fall in soil-water content from 20% to 2% meant a killing of three-quarters of the spores in the soil. Other workers (e.g. Hepple (1958) with *Mucor rammannianus*) have found that McLennan's picture of hyphae being killed by desiccation and spores being resistant is not correct for many soil forms, although it is true for a number of the surface-living dry-spored species. The chlamydospores seem exceptional, and in many cases are the primary resistant element.

Clearly spores disappear from the soil, either by death or by germination, and their numbers are restored when the various mycelia produce new crops of spores. Initially these are produced in local aggregates, yet masses of spores are seldom seen in the soil. All the evidence suggests a rapid and efficient dispersal to give a surprisingly uniform distribution of the more abundant species. This was very well demonstrated by Hinson (1954). A similar study on soil from a pasture in the Wirral, Cheshire, confirmed Hinson's results. A large piece of soil was broken across to expose a fresh face and a 1 cm. grid superimposed on the surface. Samples were taken from each square and dilution plates prepared. The six most common fungi appeared in 80% of the grid

squares. When Warcup soil crumbs were used, 62% of the crumbs contained at least 5 of the 6 commonest species. The work of Hinson suggests that animals may be primarily responsible for this efficient mixing.

When the soil is examined directly and particularly by means of soil sections (Hepple & Burges, 1956), it can be seen that different fungi exploit the soil in different ways and that a number of distinct growth patterns can be recognized. Some of these are set out below.

(i) *The Penicillium pattern.* A small piece of substrate is densely colonized by the fungus. Spore production occurs heavily over the surface of the substrate, and there is no extension of the mycelium into the surrounding soil. This growth pattern may sometimes be correlated with the ability to produce antibiotics and thus allow the fungus to dominate the localized habitat.

(ii) *The Mucor rammannianus pattern.* The fungus invades the substrate, e.g. a small dead root, utilizes the food materials, and then spreads into the surrounding soil, where it forms a zone of chlamydospores. The subsequent disintegration of the vegetative mycelium leaves a zone of resistant chlamydospores apparently unassociated with the original substrates. Hepple (1958) considers that this may give the negative rhizosphere effect reported by Thrower (1954).

(iii) *The Basidiomycete pattern.* The fungus colonizes the substrate with a long-lived mycelium, and then migrates to other substrates or to a position where it will produce fruit-bodies by means of rhizomorphs or well-developed mycelial strands.

(iv) *The Zygorrhynchus pattern.* In this the fungus appears to grow aimlessly through the soil as more or less isolated single hyphae, and does not seem to be associated with any particulate substrate. It is possible that it is growing at the expense of the small amount of organic matter dissolved in the soil solution.

(v) *The fairy-ring pattern.* The fungus migrates as a well-defined mycelial zone, causing profound microbiological and chemical changes in the soil. Careful examination does not reveal any apparent connexion between the fungus and any special substrate in the soil. A comparison (Warcup, 1951) of the soil in front of the mycelial zone and within the mycelial zone shows that about two-thirds of the soil fungi are killed by the fairy-ring, and other fungi not common in the unaffected soil become common in the mycelial zone.

It is not assumed that the above list of patterns is in any way exhaustive, and closer study will certainly reveal others. Even at this stage, however, it is clear that a proper understanding of the growth patterns is

essential for an understanding of soil mycology. A single instance may suffice. In considering the rhizosphere fungi, we do not at present have a clear picture of the formation of the stimulated population. We could imagine a heterogeneous mass of spores lying dormant in the soil, and when a root grows through the area a localized stimulation leads to the establishment of a vegetative root flora. The results of Webley *et al.* (1952) on the rhizosphere of *Atriplex* support such a view. On the other hand, the observations of Robertson (1954) on pine roots indicate that the surface flora once established grows along the root as it extends through the soil.

One of the surprising aspects of soil mycology is the difficulty which species seem to find in colonizing soil even when the normal flora has been killed or impoverished. The difficulty of an intruding species invading a well-established community is understandable, and in the work of Park (1955) one can appreciate that the native flora has already been rigorously selected as best attuned to that particular environment, and would therefore have an advantage over any invader. Where soil has been sterilized and then exposed to air, one would not expect any difficulty, particularly in view of the ease with which sterile soil is invaded in the laboratory. It may be that the growth patterns of many species limit their ability to colonize the soil under natural conditions, and it is only the spreaders such as *Trichoderma* which can readily invade.

A further aspect of the growth pattern concept which requires consideration is the sphere of influence of the fungus. A root may influence the soil around it to a distance varying from a few millimetres to several centimetres from the root surface, a distance corresponding to less than ten times the diameter of the root. In thinking of a hypha growing through the soil, we must not transfer the mental picture of the root and its relatively restricted rhizosphere to a microscale. A hypha of *Sclerotinia sclerotiorum* will grow at about 1 cm. a day. This corresponds to about 40μ per hr. Hydrogen ions released from the hyphae will diffuse through agar several millimetres in an hour in sufficient concentration to be detected by ordinary pH indicators. This corresponds to a distance hundreds of times the diameter of the hypha. If we ignore the anomalies brought about by simply magnifying the image of the fungal hyphae, this would be equivalent to a bean root affecting the soil several feet away from its growing apex. With this in mind, a growth pattern of isolated hyphae growing widely separated in the soil becomes comprehensible. They may be successfully tapping the available substrate for a distance equal to hundreds of times their own diameter.

In touching on so many aspects, I have tried to emphasize the necessity for taking a dynamic view of soil fungi. Unless we know their growth patterns, their turnover rates, and their zones of influence, we cannot hope to advance beyond the counting and listing which has occupied us for so long.

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